

Strepsirhini und den meisten anderen Mammalia – in seinem gesamten Lumen fast vollständig von olfaktorischem Epithel ausgekleidet. Das VNO aller untersuchten Primaten läßt auf Grund seiner histologischen Beschaffenheit vermuten, daß ihm eine wichtige Funktion im sensorischen Leben der Tiere zukommt. Die Befunde lassen klar erkennen, daß der VNC der Primates dem progressiv entwickelten Typus zuzuordnen ist. Charakteristisch für diese Entwicklungslinie ist ein im rostralen Abschnitt diffizil gestalteter Paraseptalknorpel, der sich zudem in diesem Bereich in der Regel in einen dorsalen und einen ventralen Ast gabelt. Beide Teile neigen zum Fusionieren mit anderen Knorpeln. Die Mehrzahl der untersuchten Primaten besitzt einen progressiv entwickelten VNC, dessen Gesamtstruktur dem anderer Mammalia bis in kleinste Details ähnelt. Bei einigen Vertretern jedoch lassen sich Besonderheiten ausmachen, die größtenteils im Zusammenhang mit der für Primates charakteristischen Umgestaltung des Fazialschädels zu sehen sind. Alle Strepsirhini besitzen ein nacktes Rhinarium, dessen Philtrum ventral mit dem Sulcus papillae palatinae kommuniziert. In diesen Sulcus aber münden die Ductus nasopalatini ein, und genau in diesem Bereich befinden sich bei einigen der untersuchten Strepsirhini Geschmacksknospen. *Tarsius* besitzt kein Rhinarium, sondern als Angehöriger der haplorhinen Primaten eine ungeteilte, behaarte, frei bewegliche Oberlippe.

References

- BAILEY, K. (1978): Flehmen in the ring-tailed lemur (*Lemur catta*). Behaviour **65**, 309–319.
- BIEGERT, J. (1957): Der Formwandel des Primateschädels und seine Beziehungen zur ontogenetischen Entwicklung und den phylogenetischen Spezialisierungen der Kopforgane. Morph. Jb. **98**, 77–199.
- BHATNAGAR, K. P.; MEISAMI, E. (1998): Vomeronasal organ in bats and primates: Extremes of structural variability and its phylogenetic implications. Microsc. Res. Tech. **43**, 465–475.
- BROOM, R. (1996): On the comparative anatomy of the organ of Jacobson in marsupials. Proc. Linn. Soc. New South Wales **21**, 591–623.
- BROOM, R. (1998): A contribution to the comparative anatomy of the mammalian organ of Jacobson. Trans. Roy. Soc. Edinburgh **39**, 231–255.
- EPPLE, G. (1976): Chemical communication and reproductive processes in nonhuman primates. In: Mammalian Olfaction, Reproductive Processes, and Behavior. Ed. by R. L. DOTY. New York: Academic Press. Pp. 257–282.
- ESTES, R. D. (1972): The role of the vomeronasal organ in mammalian reproduction. Mammalia **36**, 315–341.
- FRETS, G. P. (1912): Beiträge zur vergleichenden Anatomie und Embryologie der Nase der Primaten. Morph. Jb. **44**, 409–463.
- HEDEWIG, R. (1980): Vergleichende anatomische Untersuchungen an den Jacobsonschen Organen von *Nycticebus coucang* Boddaert, 1785 (Prosimiae, Lorisidae) und *Galago crassicaudatus* E. Geoffroy, 1812 (Prosimiae, Lorisidae). Gegenbaurs morph. Jb. **126**, 543–593, 676–722.
- HOFER H. O. (1977): The anatomical relations of the ductus vomeronasalis and the occurrence of taste buds in the papilla palatina of *Nycticebus coucang* (Primates, Prosimiae) with remarks on strepsirhinism. Gegenbaurs morph. Jb. **123**, 836–856.
- HOFER, H. O. (1979): The external nose of *Tarsius bancanus borneanus* Horsfield, 1821 (Primates, Tarsiiformes). Folia primatol. **32**, 180–192.
- HOFER, H. O. (1980): The external anatomy of the oro-nasal region of primates. Z. Morph. Anthropol. **71**, 233–249.
- HOFER, H. O.; SPATZ, W. (1963): Studien zum Problem des Gestaltwandels des Schädels der Säugetiere, insbesondere der Primaten. Z. Morph. Anthropol. **53**, 29–52.
- JORDAN, J. (1972): The vomeronasal organ (of Jacobson) in Primates. Folia morphol. (Warsz.) **31**, 418–431.
- Maier, W. (1997): The nasopalatine duct and the nasal floor cartilages in catarrhine primates. Z. Morph. Anthropol. **81**, 289–300.
- MEREDITH, M.; MARQUES, D. M.; O'CONNELL, R. J.; STERN, F. L. (1980): Vomeronasal pump: Significance for male hamster sexual behavior. Science **207**, 1224–1226.
- NIEMITZ, C. (1974): A contribution to the postnatal behavioral development of *Tarsius bancanus* Horsfield, 1821, studied in two cases. Folia primatol. **21**, 250–276.
- SASAKI K.; OKAMOTO, K.; INAMURA, K.; TOKUMITSU, Y.; KASHIWAYANAGI, M. (1999): Inosi-

- tol-1,4,5-triphosphate accumulation induced by urinary pheromones in female rat vomeronasal epithelium. *Brain Res.* **823**, 161–168.
- SCHILLING, A. (1970): L'organe de Jacobson du Lémurien malgache *Microcebus murinus* (Miller 1977) *Mém. Mus. Nat. Hist. Nat. Paris* **61**, 203–280.
- SCHILLING, A.; SERVIERE, J.; GENDROT, G.; PERRET, M. (1990): Vomeronasal activation by urine in the primate *Microcebus murinus* a 2 DG study. *Exp. Brain Res.* **81**, 609–618.
- SEITZ, E. (1969): Die Bedeutung geruchlicher Orientierung beim Plumplori *Nycticebus coucang* Boddaert 1785 (Prosimiae, Lorisidae) *Z. Tierpsych.* **26**, 73–103.
- STARCK, D. (1953): Morphologische Untersuchungen am Kopf der Säugetiere, besonders der Prosimier, ein Beitrag zum Problem des Formwandels des Säugerschädels. *Z. wiss. Zool.* **157**, 169–219.
- STARCK, D. (1982): Zur Kenntnis der Nase und des Nasenskelettes von *Tarsius* (Mammalia, Primates, Tarsiodea) *Zool. Garten N.F. Jena* **52**, 289–304.
- WIBLE, J. R.; BHATNAGAR, K. P. (1996): Chiropteran vomeronasal complex and the interfamilial relationship of bats. *J. Mamm. Evol.* **3**, 285–314.
- WÖHRMANN-REPENNING, A. (1978): Geschmacksknospen an der Papilla palatina von *Tupaia glis* (Diard. 1820), ihr Vorkommen und ihre Beziehungen zum Jacobsonschen Organ. *Gegenbaurs morph. Jahrb.* **124**, 375–384.
- WÖHRMANN-REPENNING, A. (1980): The relationship between Jacobson's organ and the oral cavity in a rodent. *Zool. Anz.* **204**, 391–399.
- WÖHRMANN-REPENNING, A. (1981): Die Topographie der Mündungen der Jacobsonschen Organe des Kaninchens (*Oryctolagus cuniculus*) unter funktionellem Aspekt. *Z. Säugetierkunde* **46**, 273–279.
- WÖHRMANN-REPENNING, A. (1982): Vergleichend-anatomische Untersuchungen an Rodentia. Phylogenetische Überlegungen über die Beziehungen der Jacobsonschen Organe zu den Ductus nasopalatini. *Zool. Anz.* **209**, 33–46.
- WÖHRMANN-REPENNING, A. (1984a): Vergleichend anatomische Untersuchungen am Vomeronasalkomplex und am rostralen Gaumen verschiedener Mammalia. *Gegenbaurs morph. Jahrb.* **130**, 501–530; 609–637.
- WÖHRMANN-REPENNING, A. (1984b): Phylogenetische Aspekte zur Topographie der Jacobsonschen Organe und der Ductus nasopalatini bei Insectivora, Primates, *Tupaia* und *Didelphis*. *Anat. Anz.* **157**, 137–149.
- WÖHRMANN-REPENNING, A. (1987): Zur Anatomie des Vomeronasalkomplexes von *Elephantulus rozeti* (Duvernoy, 1830) (Macroscelidea Mammalia). *Zool. Anz.* **218**, 1–8.
- WÖHRMANN-REPENNING, A. (1991): Functional aspects of the vomeronasal complex in mammals. *Zool. Jb. Anat.* **121**, 71–80.
- WÖHRMANN-REPENNING, A. (1993a): The vomeronasal complex – A dual sensory system for olfaction and taste. *Zool. Jb. Anat.* **123**, 337–345.
- WÖHRMANN-REPENNING, A. (1993b): The anatomy of the vomeronasal complex of the fox (*Vulpes vulpes* (L.)) under phylogenetic and functional aspects. *Zool. Jb. Anat.* **123**, 353–361.
- WÖHRMANN-REPENNING, A.; BARTH-MÜLLER, U. (1994): Functional anatomy of the vomeronasal complex in the embryonic development of the pig (*Sus scrofa* dom.) *Acta Theriol.* **39**, 313–323.

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Review

Postnatal brain size decrease, visual performance, learning, and discrimination ability of juvenile and adult American mink (*Mustela vison*: Carnivora: Mammalia)

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Abstract

The decrease in brain size to an amount of 20% during early life from the juvenile to the adult state in mink and other *Mustela* species is still poorly understood and unresolved in its general biological and functional relevance. The same holds true for the decrease in brain cavity and the flattening of the cranial vault. Since the neocortex and other brain parts with higher integrative and associative sensory and motoric functions are especially involved, the question arises as to whether these size changes have any functional consequences, i. e., are the functional capacities reduced concomitantly? This was tested for the visual system in 8 juvenile (4, 4) and 8 adult (4, 4) mink (*Mustela vison energumenos*) of wild descent using twofold-choice discrimination trials. After conditioning and testing for spontaneous side preferences, the individuals had to discriminate black dots of different sizes against a white plate from 30 cm distance. Altogether, 16 000 individual data-sets were statistically analysed for differences in visual performance, in learning velocity, and in discrimination ability. No differences occurred between the juvenile and the adult group concerning learning velocity. However, significant differences were found in discrimination ability with regard to age (juvenile mink performed better than adults) and sex (females performed better than males). These results are discussed with regard to the importance of visually guided behaviour of the species, with the behaviour of juveniles and adults in general, and with the ontogenetic decrease in mass of the central nervous tissue. According to this study, there is no indication of any functional impact of the ontogenetic reduction in brain size on the capacity of the visual system.

Key words: *Mustela vison*, ontogenesis, vision, brain size

Introduction

Unlike most other mammals, some species of the *Mustela* genus exhibit a peculiar postnatal brain ontogeny, i. e., their brain significantly decreases in size in both sexes shortly before the adult stage is reached.

This phenomenon was confirmed by brain and skull comparisons in the two domesticated forms of ranch mink (*Mustela vison* f. dom.; KRUSKA 1977, 1979, 1993) and ferret (*Mustela putorius* f. furo; APFELBACH and

KRUSKA 1979; ESPENKÖTTER 1982) as well as in wild populations of feralized ranch mink (WIG 1982, 1985) and the weasel (*Mustela nivalis*; SCHMIDT 1992). Furthermore, brain size decreases due to domestication were additionally found. This results from comparisons of adult wild American mink with adult ranch mink (KRUSKA 1996, KRUSKA and SCHREIBER 1999) as well as polecat with ferret (ESPENKÖTTER 1982). However, these changes of brain size in the course of domestication differ considerably from those in ontogenesis (KRUSKA 1987) since different brain parts are involved in the two respective processes to highly diverse degrees (KRUSKA 1993, 1996). Although not all species have been investigated so far, it can be assumed that the ontogenetic decrease in brain size appears in all *Mustela* species, including the American wild mink.

In comparative brain anatomy, intra- or interspecific differences in the mass of brain substance are usually discussed in connection with a functional increase or decrease in general central nervous capacity (KRUSKA 1988a). Because ontogenetic brain size decrease mainly occurs at an individual age from 5 to 7 months in mink, its biological relevance is especially puzzling. This is the time when the maternal family breaks up and the subadults disperse, searching for their own future home ranges (KRUSKA 1988b). A decrease in central nervous capacity at this stage of ontogeny appears unlikely.

Quantitatively, the diencephalon decreases by 9.5% in size independently of body size, but the most extreme decrease was found in the telencephalon, this being 22% smaller in size in adults compared with 5-month-old individuals. Here, the total neocortex (23%) and especially its grey matter (27%) are most dramatically decreased (KRUSKA 1993).

As these impressive size reductions affect brain parts with especially higher associative, coordinative, and integrative central nervous functions, they should have a bearing on general ethology or special behavioural performance, if functionally relevant at all. In this framework, the present study

aims at comparing the capacities of one exemplary sensory system in juvenile vs. adult wild mink (*Mustela vison energumenos*) namely visual performance, visual learning, and visual discrimination ability. The concerned brain parts, especially the occipital neocortex grey matter are especially involved in these general visual functions.

Material and methods

Animals

In total 16 (8 m, 8 f) wild mink (*M. vison energumenos*) were used in this study. Eight (4 m, 4 f) juvenile and 8 (4 m, 4 f) adult individuals were born at the Institut für Haustierkunde of the University of Kiel. They were first generation offspring of wild parents that were caught in the vicinity of Whitehorse (Yukon Territory, Canada), transported to Kiel, and kept there in large open air enclosures. The test animals were fed mainly on newly hatched chicks and housed separately in differently sized (22 m²–35 m²) wire mesh surrounded open air enclosures on natural ground with vegetation, nest boxes, and water basins. White spots different in size and pattern on the pelage of throat, breast, and belly made them individually recognizable. Additionally they were named using G as initial letter for the juveniles and F for the adults. The juvenile mink were on average 3.6 months (range: 98–117 days) old at the start of the experiments, the adult ones 11.2 months (range: 337–343 days).

Experimental arena

Twofold-choice discrimination trials were run in a simple experimental arena of wood (1.7 m in length, 0.5 m in breadth and 0.2 m in height). This arena (Fig. 1) consisted of one discrimination chamber (A) covered with wire mesh and two adjacent reward boxes (B) covered with a wooden plate. Lockable one-way swinging doors (C), 16×16 cm in dimension, allowed access to each of the reward boxes if unlocked. Plates with visual discrimination test stimuli could easily be placed on these swinging doors. There was also a partition wall (D) between these swinging doors protruding 30 cm into the discrimination chamber, thus forming a left and a right tunnel at its lower end. Entrance to the arena was only possible through a trap door (E) that could not be opened

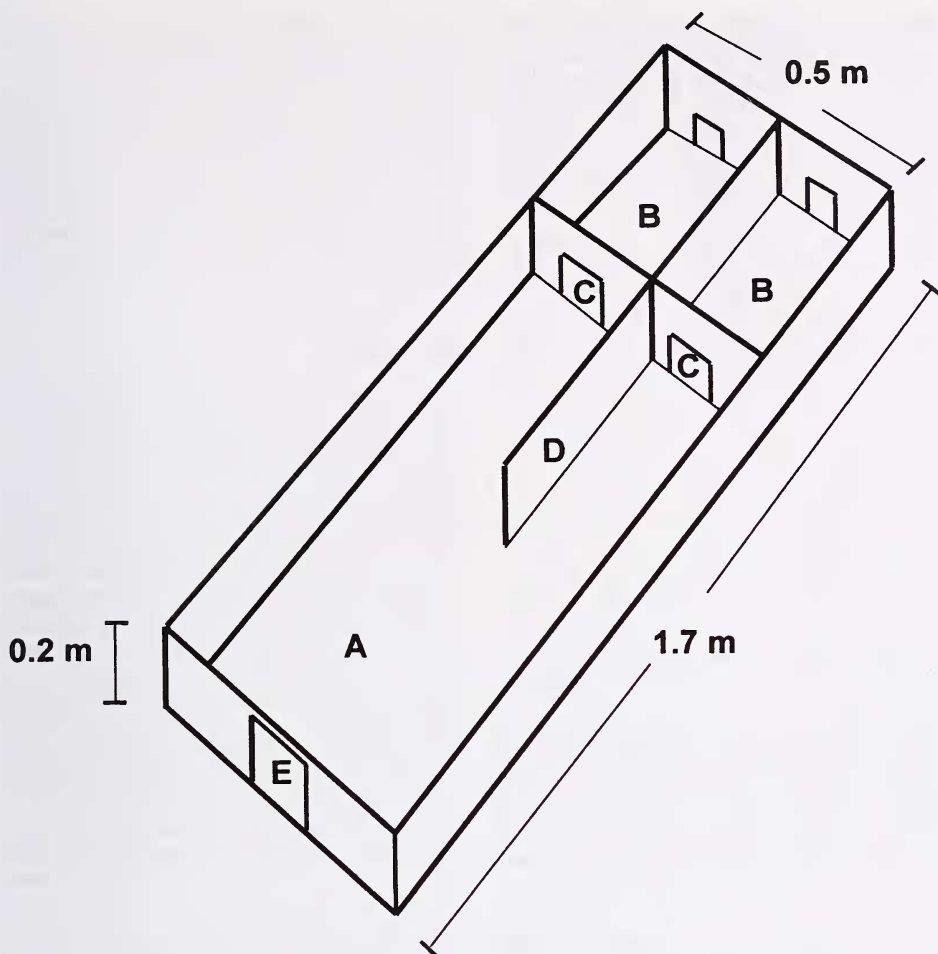


Fig. 1. Scheme of the experimental arena.

A – discrimination chamber; B – reward boxes; C – one-way swinging doors; D – partition wall; E – entrance trap door

by the animals. One-way swinging doors at the end of the reward boxes were the exits from the arena.

Experimental tests

The arena was placed in the diverse rearing enclosures of the mink, thus trials were run in accustomed environments during normal daylight. The mink were tested to discriminate visually between a totally white, blank plate and diverse white plates with central black circles of different diameter (70, 30, 25, 20, 15, 12, 9, 5, 3, and 1 mm).

The experiments were performed in four phases identical for all animals tested. During Phase 1 each of the mink was habituated to the arena and observer (K.S.). At this time all the doors were kept unlocked and pieces of food (chick parts) were randomly placed in one of the reward boxes only. Access was possible through the entrance, so the mink was conditioned to the one-way path through the arena. During Phase 2 individual side preference and its constancy were tested. Equally sized pieces of food were now offered simultaneously in both reward boxes during each trial. Each animal performed 100 runs over 2 to 3 successive days. The random right or left side choices

were recorded. During Phase 3 the animals were tested for spontaneous preference of visual stimuli. Now, for the first time the discrimination plates were affixed to the still unlocked swinging doors leading to the reward boxes both loaded with food rewards. In the first trial, the white plate was presented on one side against the white plate with a central black circle 70 mm in diameter on the other side. Each animal had to run 50 trials on one day. During these trials the position of the plates was changed from left to right and vice versa in accordance with the schedule of GELLMAN (1933). Hereby it was ensured that (1) the subsequent side (left/right) was unpredictable to the animals, (2) no plate was offered more than maximally three times on the same side in consecutive trials to avoid possible side preferences, and (3) both sides (left/right) occurred overall at the same frequency. Phase 4 finally represents the entire tests aimed at for visual discrimination and learning. In this, the white plate was designated the incorrect choice and consequently the swinging door bearing this plate was locked during all following trials, although the associated reward box always contained equal quantity of meat reward. This controlled for choices made on possible olfactory cues.

In each trial, the mink had to make their decision at a 30 cm distance from the swinging doors and choices were evaluated by the observer (K. S.) as positive or negative. These evaluations followed stringent criteria. Choices were counted as positive only in cases where animals ran to the positive sign immediately after entrance into the discrimination chamber. In cases where they showed preference for the wrong side or started to move towards the negative stimulus, this was counted as a negative choice even if they seemed to recognize the failure and corrected their choice later.

Trials with the same plates were run 50 times on one day by each of the mink followed by a day of relaxation and 50 trials on the subsequent day. A higher number of trials daily led to erratic performance in later trials, probably due to satiation after the positive rewards.

The time point at which conditioning to the 70 mm circle had occurred was very clearly recognisable through a change in behaviour. From that moment on, mink moved rather rapidly and directly towards the correct sign. The number of runs preceding this conditioning was taken as a measure of individual learning velocity. The entire 100 discrimination trials with the 70 mm circle were conducted after conditioning had taken place. Only after completing the 100 trials on the

70 mm circle during two days the next smaller sign was tested in the same manner, regardless of the animal's prior performance, and the trials continued in the same way for all smaller circles. The order in which the individual animals were tested and the time of day (08.00 h–12.00 h) the trials were run was constant throughout the experiment. Each of the 16 mink therefore completed a total of 1000 test trials. Thus, altogether 16000 runs yield the data base for statistical treatment.

Data analysis

Choices during Phase 1 were not analysed statistically. Habituation to the apparatus and conditioning to find food were continued until the animals performed efficiently. Choices of Phase 2 and 3 were treated statistically. The significance of spontaneous preferences for side (right/left; Phase 2) and visual stimuli (stimulus present/absent; Phase 3) was assessed by a replicated goodness-of-fit χ^2 -test. During the learning phase, mink were considered as trained to the visual stimulus if they correctly chose 63 out of 100 trials. This corresponds to a probability of $p = 0.99$, i. e. the mean rate of correct choice is significantly larger than expected at random (= the lower limit of the 99% confidence interval for the mean rate of correct choice exceeds 0.5; SOKAL and ROHLF 1995). The total of 16000 individual trials of the entire Phase 4 was jointly analysed using a log-linear model for frequency data (BISHOP et al. 1975; SOKAL and ROHLF 1995). By this approach we examined the influences of age, sex, and sign size on the discrimination efficiency as well as the various interactions among these factors.

Results

General behaviour of the individuals

The individual mink differed slightly in general behaviour prior to as well as during the experiments. The adult mink, e. g., were accustomed to their enclosures for a longer period and were minimally disturbed by humans. During Phase 1, they acted rather hesitantly and shyly. The juveniles, in contrast, seemed to be more bold and curious. Adult individuals required up to 20 sec. for a run through the experimental arena, while juveniles clearly operated faster, on average only 4–8 sec. per run. Apart from this, some

individuals of both age groups were especially shy, labile, and less concentrated during the trials (Gira, Giwa, Feka), while others remained comparably calm and difficult to motivate (Galbus, Fabea, Felia, Fedor, Falkano, Fargo). In contrast, still others acted very excited, concentrated, and fast. They often vocalised the typical twitters of excitement (Gilia, Galicia, Gaius, Gagarin, Godu, Fiona, Fibius) during trials. Sex-specific differences were especially marked. In cases of a wrong decision, for example, adult males tended to be aggressive and bit, scratched and tore at the locked entrance to the reward box but such behaviour was never observed in females. In comparable situations, females only corrected their erroneous decision by running to the positive sign with the food reward. Thus, although such a choice was negatively evaluated for the trial, females showed a somewhat greater plasticity in such situations. This is also reported for many other mustelids. Females, both adults and juveniles, were also more active in general compared to males, especially during the habituation and conditioning phases. Males were clearly less motivated and comparably disinterested. All the animals, however, completed all trials although in individually different ways.

Side preference and spontaneous preference for visual stimuli

Summarised results of the test for spontaneous side preference and side constancy of choices are given in table 1. There was no significant overall side preference (replicated goodness-fit: $\chi^2_{\text{pooled}} = 0.25$, $df = 1$, $p = 0.617$), but the side preference was significantly heterogeneous among individuals (replicated goodness-fit: $\chi^2_{\text{heterogeneity}} = 40.00$, $df = 15$, $p < 0.001$). This was caused by four individuals exhibiting a spontaneous side preference, significant at $p < 0.05$. Albeit this preference was only slight (62:38 at maximum) and symmetrical (two individuals preferred left, two right), the potential influence of individual side preference on the visual discrimination effi-

Table 1. Individual side preference prior to conditioning (100 runs per animal)

Age	Sex	Individual	side choice	
			left	right
juvenile	female	Gilia	56	44
		Gira	41	59
		Galicia	38	62
	male	Giwa	40	60
		Galbus	54	46
		Gaius	39	61
adult	female	Godu	62	38
		Gagarin	42	58
		Fiona	50	50
		Felia	62	38
		Feka	50	50
	male	Fabea	52	48
		Fedor	56	44
		Falkano	56	44
		Fibius	54	46
		Fargo	58	42

ciency was estimated in a separate log linear model.

Most mink showed no preference for either a blank white plate or a 70 mm black circle. Based on 50 runs per animal and a significance level of $p = 0.05$, only two individuals seemed to slightly prefer the circle, while three others did so with the white plate.

Learning velocity

Regarding individual learning velocity, the juvenile mink clearly showed less variability of run numbers (range: 57 to 95) than the adults (range: 51 to 200) prior to conditioning (Tab. 2). This was caused by two particular adults (Fibius, Feka) learning very slowly, with 200, respectively, 150 trials prior to conditioning. However, all the other adults reached values within the variance of the juveniles. Over all, there were no significant differences among the four groups, i.e., juvenile and adult mink of both sexes (Kruskal-Wallis-Test: $H = 4.83$, $df = 3$, $p = 0.185$). Thus, learning velocity during conditioning of individual mink can be considered identical and independent of age and sex.

Table 2. Learning velocity during conditioning (runs per animal until they were considered conditioned; see methods for details).

Age	Sex	Individual	number of runs
juvenile	female	Gilia	89
		Gira	95
		Galicia	57
	male	Giwa	73
		Galbus	75
		Gaius	79
		Godu	80
adult	female	Gagarin	71
		Fiona	51
		Felia	81
	male	Feka	150
		Fabea	80
		Fedor	76
		Falkano	82
		Fibius	200
Fargo	81		

Table 3. Significant factors determining visual discrimination ability, given as % variation explained (result of a log-linear model analysis).

Factor	DF	χ^2	p	% of variation explained
Sex	1	13.25	<0.001***	4
Age	1	46.65	<0.001***	14
Sign size	9	116.41	<0.001***	35
Interaction sex vs. age	1	10.32	0.001***	3
Interaction age vs. sign size	9	45.41	<0.001***	14
total explained variation	-	-	-	70
unexplained variation	-	-	-	30 [#]

[#]From 30% unexplained variation, 10% could be attributed to individual side preferences (as indicated by a separate log-linear model).

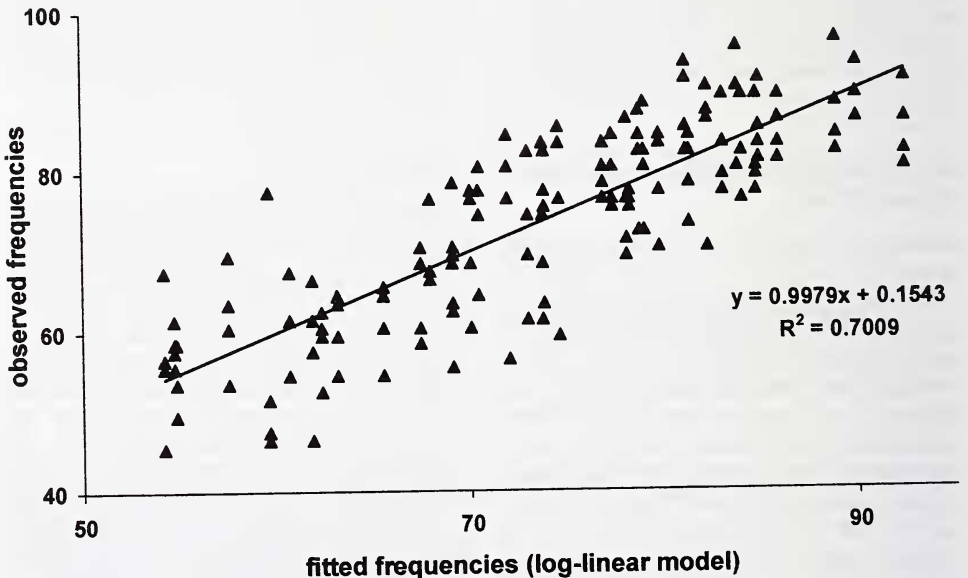


Fig. 2. Correlation between fitted and observed frequencies of correct choices in the visual discrimination experiment, when sex, age, sign size and the two interactions sex vs. age and age vs. sign size are included in the log-linear model.

Table 4. Individual visual discrimination efficiencies of the juvenile and the adult mink. Numbers of positive choices are presented out of 100 runs on each of the black circles different in diameter. Grey shaded fields indicate performances below the significance level of 63%. Mean values of groups (\bar{x}) and standard deviations (SD) are also given.

age/sex	name	Diameter (in mm) of black circle positive sign									
		70	30	25	20	15	12	9	5	3	1
juvenile ♀	Gilia	77	82	89	81	89	89	87	75	76	53
	Gira	76	80	79	86	93	82	90	77	85	49
	Galicia	75	88	77	89	86	89	86	82	83	58
	Giwa	75	72	80	83	93	76	70	63	59	49
juvenile ♂	Galbus	80	69	90	85	84	83	78	69	61	55
	Gaius	75	71	80	83	82	77	73	61	68	56
	Godu	76	86	95	91	96	79	84	74	74	45
	Gagarin	84	76	80	81	88	89	82	82	83	67
juvenile \bar{x}		77.3	78.0	83.8	84.9	88.9	83.0	81.3	72.9	73.6	54.0
	SD	2.99	6.65	6.16	3.40	4.54	5.12	6.57	7.44	9.46	6.34
adult ♀	Fiona	86	77	83	84	80	77	67	70	65	52
	Felia	82	83	80	82	84	80	76	78	64	62
	Feka	80	70	76	87	76	64	76	69	60	60
	Fabea	91	84	78	72	56	74	66	55	54	59
adult ♂	Fedor	91	76	70	69	63	61	46	54	63	58
	Falkano	93	77	68	63	59	46	47	61	60	57
	Fibius	82	68	60	68	64	57	51	61	53	55
	Fargo	85	60	58	62	54	66	77	67	69	61
adult \bar{x}		86.3	74.4	71.6	73.4	67.0	65.6	63.3	64.4	61.0	58.0
	SD	4.58	7.50	8.63	9.08	10.7	10.5	12.5	7.61	5.10	3.08
females \bar{x}		80.3	79.5	80.3	83.0	82.1	78.9	77.3	71.1	68.3	55.3
	SD	5.43	5.74	3.86	4.85	11.3	7.69	8.81	8.27	10.9	4.79
males \bar{x}		83.3	72.9	75.1	75.3	73.8	69.8	67.3	66.1	66.4	56.8
	SD	6.04	7.22	12.6	10.3	14.5	13.7	15.3	8.28	8.69	5.80

Visual discrimination efficiency

According to the log-linear model, the key determinant of the visual discrimination efficiency was the sign size (accounting for 35% of the variation in discrimination efficiency), followed by age and sex, explaining 14% and 4% of the variation found, respectively (Tab. 3). Two two-factor interactions were significant, the interactions age vs. sign size and age vs. sex, accounting for 14% and 3% of the found variation in discrimination efficiency, respectively. Altogether, these factors explained 70% of the present variation and yielded a good fit between observed discrimination efficiency and values expected by the model (Fig. 2). Of the remaining 30% variation unexplained, about 10% can be attributed

to individual side preferences (as indicated by a separate log-linear model), while the remaining 20% apparently represents individual differences and stochastic errors. Individual efficiencies to discriminate differently sized black circles are summarized in table 4. Evidently, the mink were generally unable to recognize a black dot sign 1 mm in diameter (except for one juvenile male). Additionally, six out of the 16 animals had also difficulties to discriminate the 3 mm sign. Thus, to discriminate a motionless sign of this size from a distance of about 30 cm may be problematical for mink in general. In this context, adult males are peculiar because of their different efficiencies from sign to sign. This specifically poor performance of adult males – especially with smaller signs – is the apparent expla-

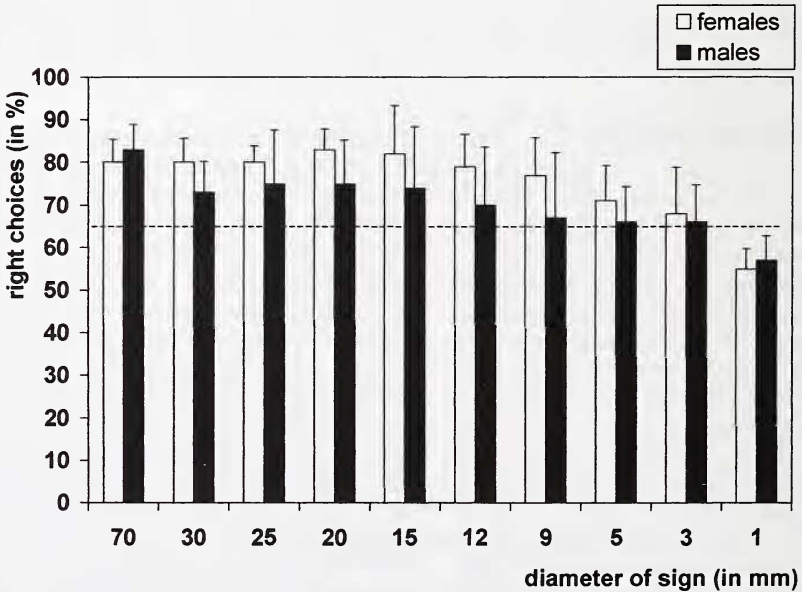
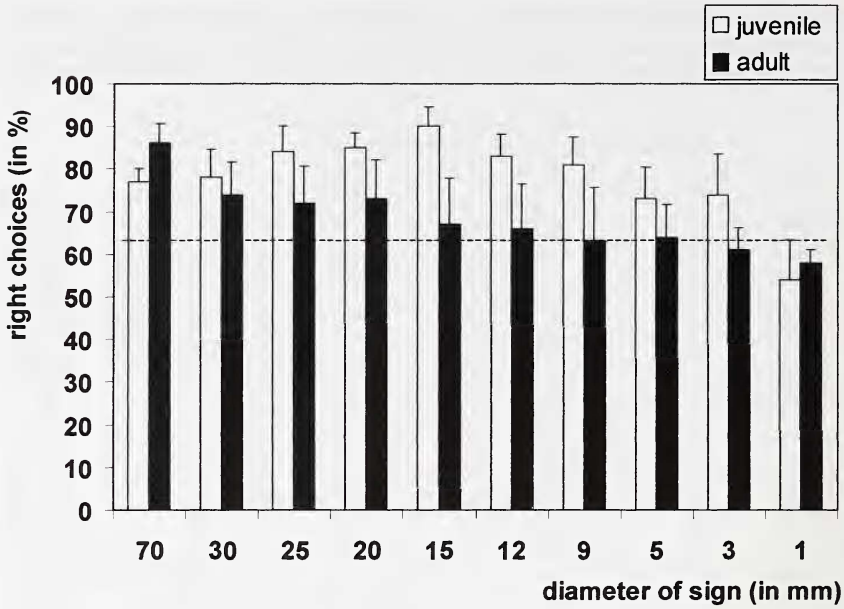


Fig. 3. Arithmetical means of positive choices for the differently sized signs of juvenile vs. adult and of female vs. male mink. Dotted line indicates the 63% level; vertical lines indicate standard deviations.

nation for the two significant factor interactions (age vs. sign size; age vs. sex). Very obviously their minor concentrations on the tasks are reflected in these results. Nevertheless, except for the smallest signs mink chose on average significantly more frequent correct than wrong, regardless of their sex and age (Fig. 3).

Discussion

In connection with the aim of this study it seems worth mentioning what is known about the importance of visually guided behaviour in the biology of the investigated species. Thus mink – like other *Mustela* species – are in general basal carnivores with only little anatomical specialisation (EWER 1973). They are predators which regionally and seasonally prey on different vertebrates and invertebrates, hunting and chasing on land but since they are adapted to a semi-aquatic life style larger parts of food are also taken from rivers, lakes, or the sea. They are very efficient hunters, reacting quickly both in air and under water. They are thus dependent on their sensory organs for detection of prey, chasing, and killing but also for recognizing their own predators. Concerning their general orientation, they often are said to be sensory-guided mainly by olfaction followed by hearing and then by vision. However, such ranking in the importance of sensory organs and central nervous circuits for species-specific biological peculiarities seems rather meaningless since according to our own observations and those of others as well, mink very efficiently hunt fish in muddy waters even during dark times of the day and also in clear, reflecting waters during bright sunshine. Thus, it can be suggested that at least during these hunts they are mainly guided by sensory functions of the vibrissal system rather than by olfaction, hearing, or vision. Therefore, it seems more likely to conclude that all sensory systems are of certain importance for the biology of mink with different priorities at given situations. However, mink have well developed eyes and

differentiated central nervous visual structures. The duplex retina is built up by highly differentiated and extremely polarized rods and cones, with the rods being more numerous (DUBIN and TURNER 1977; BRAEKEVELT 1990; STEFFEN 2000). The lateral geniculate body as the main termination nucleus of visual perception is well differentiated (GUILLERY et al. 1979) showing certain laminae and an input of approximately about 75% to 80% crossed and 20% to 25% uncrossed fibres (SANDESON 1974; SANDESON et al. 1975). Accordingly, the striate area at the occipital lobe of the neocortex is well organized and histologically clearly distinct from surrounding areas (LEVAY et al. 1987; GUILLERY and OBERSDORFER 1977; GUILLERY et al. 1979). In relative size this highest sensory field accounts for about 6.8% of the total neocortical grey matter (own preliminary results). All these anatomical characters can without doubt be indicative for what normally is called good vision in contrast to poor eyesight. This is also confirmed by ethological and physiological tests and findings (DUNSTONE 1993; DUNSTONE and SINCLAIR 1978 a, b). Acuity of predators for stationary objects (like dots) is less poorly developed than for moving objects. A recognition of black dots different in size might therefore be of limited importance for the biology of a species but at least documents its visual acuity and functional complexity. However, as our results indicate the animals acted in response to these stimuli and they were able to discriminate different sizes. Thus, the reactions of the animals on the experimental tasks may serve as a measure for functional sensory and central nervous capacities.

In order to uncover a probable relationship between the size of a brain structure and its complex functional capacity, the quantitative structural changes of central nervous tissue from juvenile to adult mink (KRUSKA 1993) can be correlated with quantitative functional differences as resulted from the visual test procedures presented here. Concerning such a relation, however, no unequivocal conclusions can be drawn, as apparent correlation may appear coincident

tally. As example, juvenile mink, known to possess significantly larger neocortical and diencephalic brain regions, generally showed significantly better results in reactions to visual discrimination tasks than adults both in female and male individuals. Consequently, this could be considered an indication for greater functional capacities of juveniles due to larger central nervous structures. This is, however, contradicted by the finding that learning velocity is independent of age. On the other hand, differences were observed among sexes concerning their discrimination ability, although mass and proportioning of the brain did not differ among sexes, either within the larger brained juveniles or within the adults (KRUSKA 1993). For these reasons, the postnatal overshooting of brain size has most probably no functional consequences for the biology of mink, at least not for the capabilities of the visual system. The fact that

juvenile individuals are more playful, curious, easier to be conditioned, open for learning and consequently more efficient in behavioural experiments than adults is commonly known from many other mammalian species (WÜSTEHUBE 1960; GOETHE 1964; RENSCH 1973; TEMBROCK 1982) including those with normal brain size development. Thus, the postnatal brain size decrease most probably has no effects on visual functions and still remains unsolved in its biological relevance.

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Zusammenfassung

Postnatale Hirngrößenabnahme, visuelle Leistung, Lernen und Unterscheidungsvermögen von juvenilen und adulten amerikanischen Minken (*Mustela vison*: Carnivora: Mammalia)

Die Abnahme der Hirngröße im Ausmaß von 20% während der Entwicklung vom juvenilen zum adulten Stadium beim Mink und anderen *Mustela*-Arten ist nach wie vor wenig verstanden und in ihrer generellen biologischen und funktionellen Bedeutung ungeklärt. Entsprechendes gilt für die einhergehende Verkleinerung des Hirncavums, vornehmlich bedingt durch Abflachung des Hirnschädels. Da der Neocortex und andere Hirnteile mit höheren integrativen und assoziativen sensorischen und motorischen Funktionen besonders betroffen sind, erhebt sich die Frage, inwieweit diese Größenänderungen funktionelle Konsequenzen haben; d. h. sind funktionelle Kapazitäten dieser Hirnstrukturen gleichzeitig gemindert? Dieses wurde für das visuelle System bei 8 juvenilen (4,4) und 8 adulten (4,4) Nachkommen von Minken (*Mustela vison energumenos*) aus freier Wildbahn unter Einsatz einer Zweifach-Wahl-Apparatur getestet. Nach Konditionierung und Test auf spontane Seitenstetigkeit mußten die Individuen schwarze Punkte unterschiedlicher Größe von weißen Flächen aus 30 cm Entfernung unterscheiden. Insgesamt wurden 16 000 individuelle Datensätze erhoben und statistisch auf Unterschiede in visueller Leistung, Lerngeschwindigkeit und Unterscheidungsvermögen analysiert. Es ergaben sich keine Unterschiede in der Lerngeschwindigkeit zwischen juvenilen und adulten Individuen. Allerdings resultierte ein signifikanter Einfluß von Alter (juvenile Tiere zeigten bessere Ergebnisse) und Geschlecht (Fähen zeigten bessere Ergebnisse) im visuellen Unterscheidungsvermögen. Diese Ergebnisse werden im Zusammenhang mit der biologischen Bedeutung des Gesichtssinns für diese Tierart, mit generellen Verhaltensunterschieden zwischen juvenilen und adulten Individuen und mit der ontogenetischen Abnahme zentralnervöser Masse diskutiert. Im Hinblick auf diese Untersuchungen gibt es keine Anzeichen für einen funktionellen Zusammenhang zwischen der ontogenetischen Hirngrößenabnahme und Leistungsfähigkeit des visuellen Systems.